

DIURNAL TIME-ACTIVITY BUDGETS OF WINTERING CANVASBACKS IN LOUISIANA

WILLIAM L. HOHMAN AND DAVID P. RAVE¹

ABSTRACT.—We determined diurnal time-activity budgets of Canvasbacks (*Aythya valisineria*) at Catahoula Lake and at the Mississippi River Delta, Louisiana, from December 1987 to March 1988. Canvasback feeding, resting, locomotory, and comfort activities varied by month and location with a month-location interaction. Moreover, the percentage of time spent feeding varied by sex with a month-sex interaction. Study site differences in the time-activity budgets of wintering Canvasbacks may be related to characteristics of their foods, foraging mode, disturbance level, and physical features of habitats at the two study sites. Canvasbacks wintering in Louisiana generally spent less time feeding and more time resting during the day than they did in Mississippi or coastal South Carolina. Levels of agonistic behavior were lower than those observed in South Carolina. We found no evidence of male dominance of female Canvasbacks in Louisiana. *Received 14 Dec. 1989, accepted 22 Mar. 1990.*

Overwinter and annual survival probabilities of waterfowl may be influenced by their relative body condition in winter (Haramis et al. 1986, Hepp et al. 1986). Further, it has been suggested that waterfowl recruitment is correlated with winter body condition (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1986). Energy relationships between a bird and its habitat, as reflected in its body condition relative to other individuals, are mediated through the time-activity budget of the bird (Paulus 1988). Whereas many aspects of the behavior (Alexander and Hair 1979; Alexander 1980, 1987), nutritional ecology (Perry 1982, Perry et al. 1986, Lovvorn 1987), and population biology (Nichols and Haramis 1980a, b; Haramis et al. 1985) of Canvasbacks (*Aythya valisineria*) wintering in the Atlantic Flyway have been investigated, Canvasbacks wintering elsewhere, especially in the Gulf of Mexico region, have been inadequately studied. Louisiana is a major wintering area for Canvasbacks, providing habitat since 1985 for >25% of the continental population (U.S. Fish and Wildlife Service [USFWS], Office of Migratory Bird Management, unpubl. data). We report here on time-activity budgets of wintering Canvasbacks at two sites in Louisiana. Canvasback activities are compared among wintering populations and between the wintering and migration periods.

¹ U.S. Fish and Wildlife Service, National Wetlands Research Center, Baton Rouge Field Research Station, % Center for Wetland Resources, Louisiana State Univ., Baton Rouge, Louisiana 70803-7500. (Present address DPR: 409 Walnut Street, Grand Forks, North Dakota 58201.)

STUDY AREAS AND METHODS

This study was conducted at Catahoula Lake (CL) in central Louisiana (31°15'N, 92°00'W) and at the Mississippi River Delta (MRD) in southeastern Louisiana (29°15'N, 89°15'W). These two sites were selected from nine that traditionally are used by wintering Canvasbacks because of their locations (inland vs coastal) and high use. Sixty-eight to 74% of all Canvasbacks observed on monthly statewide surveys in winter 1987–1988 were recorded on these two sites (D. W. Woolington, USFWS, unpubl. data). Maximum numbers of Canvasbacks censused were 58,000 on CL and 14,000 on the MRD.

CL is a large (12,150 ha), swallow basin in the Mississippi River floodplain. The lake is drained in the summer to stimulate plant growth and flooded in the fall to provide waterfowl habitat and hunting opportunity (Zwank et al. 1985). Local rainfall or flooding of the Mississippi River caused by major runoff events upstream may produce abrupt changes in lake levels. For example, in winter 1987–1988, lake levels increased 3.9 mm in four days following locally heavy rains. Water depth at the center of the lake ranged from 0.2 m to 5.5 m and averaged 3.1 ± 0.22 m ($\bar{x} \pm \text{SE}$) during the study.

The deltaic plain of the Mississippi River is a highly dynamic and complex wetland system (Bahr et al. 1983). Water levels in the marsh change daily and seasonally. Marsh flooding is directly influenced by tidal changes and stages of the Mississippi River. The Mississippi River exceeds flood stage about 25% of the year. River stage is generally highest in late winter and lowest in summer. High and low tides occur once each day with a maximum range of 0.3 m. Wind also exerts a major influence on water levels in the marsh. Onshore winds may impede river flow and cause back-flooding into the marsh, whereas sustained offshore winds tend to reduce marsh water levels.

Feeding sites used by Canvasbacks at the two study locations differed markedly from each other and from those used elsewhere by wintering Canvasbacks (e.g., San Francisco Bay, Chesapeake Bay, coastal North Carolina). At CL, open water feeding sites as deep as 6 m were used by Canvasbacks, but at the MRD, birds used deltaic splays (i.e., accreting mudflats receiving shallow, intermittent flooding) almost exclusively. Deltaic splays were pitted with shallow depressions generally <2 m in diameter. These depressions contained water even at low tide and presumably were the result of disturbance by grazing nutria (*Myocastor coypus*).

We observed Canvasback behavior at the two study sites during the first ten days of each month from December 1987 to March 1988. Our procedures generally followed those used on wintering and spring-staging Canvasbacks by Alexander (1980) and Lovvorn (1987). Three persons (two observers and one data recorder) conducted continuous observations from elevated platforms throughout the daylight period. Observations began with the random selection of a focal individual. The focal bird of a given sex was identified by selecting a random number (1–100) and counting that number of individuals of the same sex from the left to the right edge of the observation area (i.e., field of view including all birds for which sex and activity could be reliably determined). Once selected, the focal individual was observed for 5 min, during which instantaneous behavior was recorded at 15-sec intervals (20 observations per focal bird) (Weins et al. 1970). At the end of the 5-min observation period, another bird was chosen by selecting the fifth bird of the same sex to the right of the previous focal bird. If fewer than five birds were present in that field of view, then the first individual of the same sex in the next field of view to the right was chosen. When the entire observation area had been scanned, observations were resumed with the random selection of a bird as described above. Systematic scanning of Canvasback flocks, as outlined above, was followed to ensure that observations were obtained from throughout the observation area.

We categorized Canvasback activities as follows: *feeding*—behavior associated with food search (e.g., preparation for diving, diving and tipping-up), capture and handling; *resting*—inactive birds with head positioned low on chest, bill setting on breast, or sleeping with bill tucked into scapular feathers; *locomotion*—birds swimming or in flight; *comfort*—behavior associated with body maintenance; *alert*—bird vigilant, head held off shoulders but not performing any other activity; and *other*—behavior associated with courtship and mating, and agonistic behavior ranging from threats and avoidance to bill thrusts, chasing and fighting (Alexander 1980). Focal individuals flying outside the observation area were assumed to be in flight for the balance of the 5-min period, and observations were resumed at the start of the next period from the location where the bird took flight. Pairing status of the focal individual was assigned at the end of the 5-min observation period. Paired individuals were those showing active association; that is, copulation, mutual display, female tolerance of male, or nonrandom spacing. All agonistic displays within the field of view of the spotting scope were recorded (i.e., species and sex of participants, and outcome of interaction). Sex of all Canvasbacks in the observation area was determined at least once daily to calculate the ratio of males to females. Disturbances caused by human activities were noted.

We used a three-way analysis of variance including all interactions to assess the effects of sex, month, and study site on individual activities of wintering Canvasbacks (PROC GLM, Statistical Analysis System to perform calculations; SAS Institute, Inc. 1987). Because analyses of raw data and arcsine square-root transformed data ($p^{1/2}$) yielded similar results, we here report results based on raw data only. We used χ^2 -tests to analyze agonistic behavior by sex and study site (Conover 1980). Expected encounter rates between sexes were derived from sex-ratio data.

RESULTS

Time-activity budgets of Canvasbacks at CL and the MRD were based on about 350 hours of behavioral observations made on 4245 focal individuals. All Canvasback activities varied by month and location with a month-location interaction ($P < 0.025$). Moreover, the percentage of time spent feeding varied by sex ($P = 0.0335$) with a month-sex interaction ($P = 0.0001$). Females fed more than males in early and late winter (Fig. 1). Except for feeding, however, activity patterns of male and female Canvasbacks were similar at both sites.

Canvasbacks at the MRD fed more than those at CL, especially in midwinter ($P < 0.0001$; Fig. 1). Resting was higher at CL than at the MRD in midwinter, but the reverse was true in December and March ($P < 0.0001$; Fig. 1). Time spent performing locomotory activities changed differently at the two study sites through the winter ($P < 0.0001$; Fig. 1). Canvasbacks swam more at CL than at the MRD in all months except January ($P \leq 0.0001$; Fig. 1). Time in flight averaged $< 1\%$ at both study sites in winter 1987–1988. Comfort activities declined after December at both study sites, but were consistently higher at CL than at the MRD ($P \leq 0.0001$; Fig. 1).

Agonistic behavior was observed at both study sites in all months, but only in February did the percentage of time spent in intraspecific aggres-

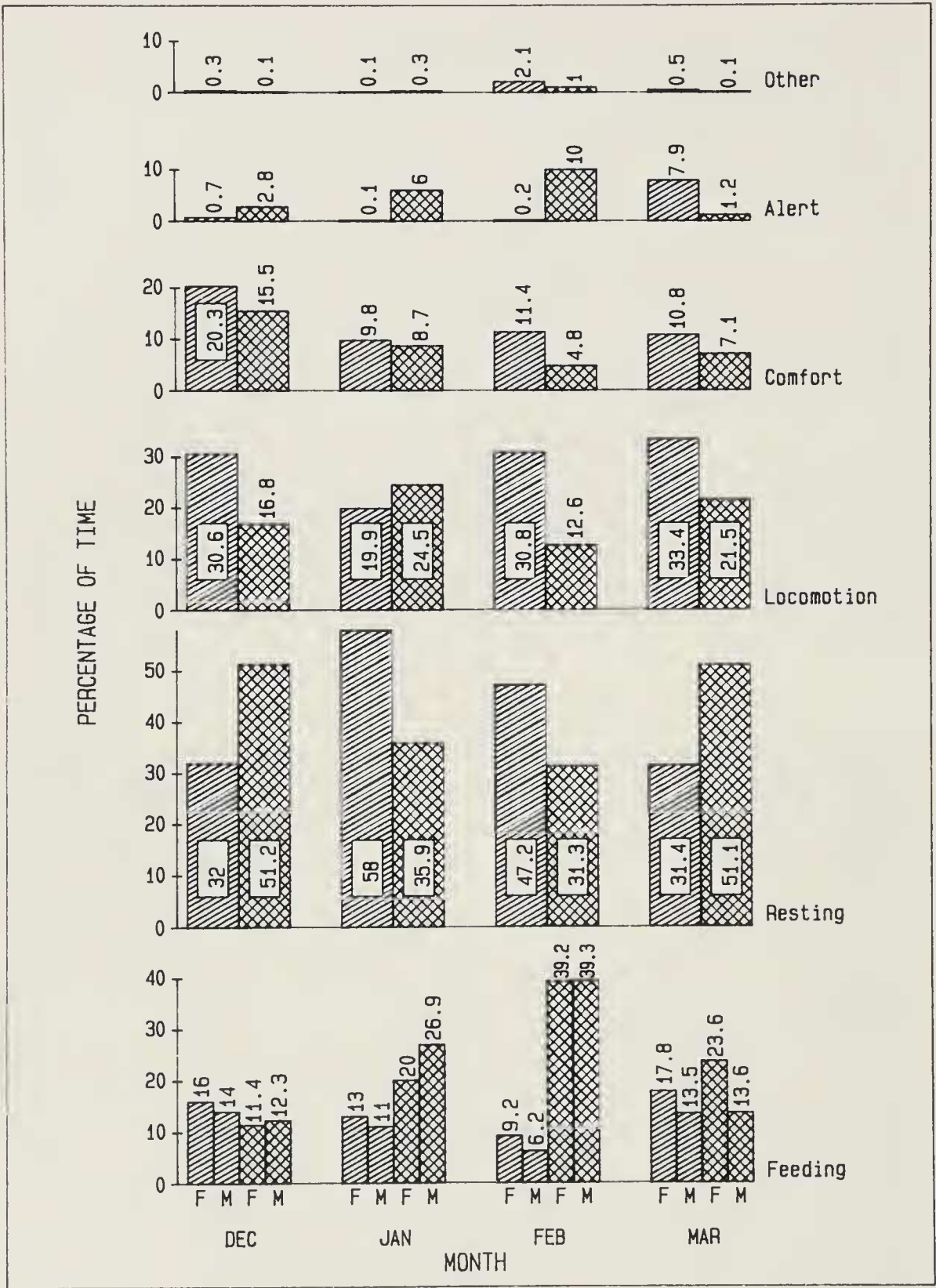


FIG. 1. Time-activity budgets of male (M) and female (F) Canvasbacks at Catahoula Lake (single-hatching) and the Mississippi River Delta (cross-hatching), Louisiana, in winter 1987-1988.

TABLE 1
DIURNAL TIME-ACTIVITY BUDGETS OF NONBREEDING CANVASBACKS

Period Location	Activity ^a				References
	Feeding	Resting	Movement	Comfort	
Fall-migrating					
Wisconsin	19	35	17	15	Takekawa (1987)
Wintering					
Mississippi	23	30	24	20	Christopher (1987)
South Carolina	33	34	20	11	Alexander (1980)
Louisiana					
Catahoula Lake	13	42	29	13	This study
Mississippi Delta	23	42	19	9	This study
Spring-migrating					
Wisconsin	39	22	8	13	Lovvorn (1987)
Ontario	36	17	14	15	Lovvorn (1987)

^a Percentage of time spent performing activity.

sion exceed 0.5%. Levels of Canvasback aggression at the two study sites were similar, but patterns of aggression differed. Female-female aggression at the MRD was higher than predicted ($N = 271$ encounters; $\chi^2 = 13.6$; 3 df; $P < 0.005$). At CL, the occurrence of male-male interactions was low, and male initiation of aggression with females was higher than predicted ($N = 125$ encounters; $\chi^2 = 36.8$; 3 df; $P < 0.001$).

Interspecific aggression mostly involved American Coots (*Fulica americana*) associated with feeding Canvasbacks, and, to a lesser extent, Ruddy Ducks (*Oxyura jamaicensis*), Ring-necked Ducks (*Aythya collaris*), Northern Pintails (*Anas acuta*), American Wigeons (*Anas americana*), Gadwalls (*Anas strepera*), Green-winged Teals (*Anas crecca*), and grackles (*Quiscalus* spp.).

Courtship activities were rarely observed in wintering Canvasbacks in Louisiana. Pair bonding was evident in fewer than 1% of Canvasbacks observed in late winter.

DISCUSSION

Diurnal time-activity budgets of Canvasbacks vary seasonally and geographically (Table 1). We found that Canvasbacks wintering at CL and the MRD generally spent less diurnal time feeding and more time resting than did Canvasbacks wintering in Mississippi or coastal South Carolina (Table 1). Spring-migrating Canvasbacks fed more, but rested and moved less than wintering birds (Table 1). Time-activity budgets of wintering

Canvasbacks in Louisiana were most similar to those of fall-migrating birds (Takekawa 1987), but, because pauses occurring immediately before dives were classified as resting (vs feeding), time spent feeding probably was underestimated for fall-migrants (J. Y. Takekawa, USFWS, pers. comm.).

Study site differences in time-activity budgets of wintering Canvasbacks may be related to characteristics of their foods, foraging mode, disturbance levels, and physical features of habitats at the two sites. Diets of wintering Canvasbacks at CL and the MRD were similar in at least four respects: (1) they consisted of more than 97% plant material, (2) below-ground plant parts made up the largest portion (94 aggregate percent dry mass) of the diet, (3) dietary diversity was low, and (4) diet composition was independent of age, sex, or month (Hohman et al. 1990). Canvasbacks are behaviorally and morphologically specialized to feed on subterranean plant parts (Goodman and Fisher 1962, Tome and Wrubleski 1988). These foods contributed about 94% of the Canvasback diet both at CL and the MRD; however, the mode of foraging for below-ground foods differed between study sites. At the MRD, foraging birds were widely dispersed over mudflats (one bird per disturbed site) and fed in shallow water by tipping-up. In contrast, Canvasbacks at CL associated in large flocks and dived as deep as 6 m to obtain food.

Canvasbacks at the MRD seemed to forage around the perimeter of disturbed sites (i.e., enlarging disturbed sites), excavating with their feet and bill into previously undisturbed mudflats, where dry mass of subterranean plant parts was four-times greater than that within disturbed sites (Hohman et al. 1990). Aggressive defense of feeding sites was common at the MRD, as it was among diving ducks feeding on banana water-lily (*Nymphaea mexicana*) in coastal impoundments in South Carolina (Alexander 1980). Canvasbacks presumably do so because food resources at these sites are economically defensible. Habitat conditions favoring food resource defense by Canvasbacks at the MRD include shallow water depth, patchy distribution of food, considerable time and energy expenditures required to access food items, and large potential gain from foraging effort.

In winter, mudflats at the MRD are devoid of residual vegetation and are covered by a hardened crust. Disturbed sites may provide cues of food distribution and abundance to foraging Canvasbacks (indicating where foods may be found). Moreover, Canvasbacks feeding at the edge of disturbed sites avoided having to penetrate the sediment crust and thus may have foraged more efficiently than birds feeding in undisturbed areas. Although immature Herring Gulls (*Larus argentatus*) were observed harassing feeding Canvasbacks at the MRD (W. L. Hohman, pers. obs.), predation risks apparently are low and do not place individual foragers

at a disadvantage. Densities of subterranean plant foods at the MRD (Hohman et al., in press) and especially at CL (Wills 1965), may be high relative to those at other major Canvasback wintering areas, such as Chesapeake Bay (Orth and Moore 1981) and coastal North Carolina (Lovvorn 1987). Flock feeding probably was facilitated by the high density of chufa flatsedge (*Cyperus esculentus*) tubers at CL. Moreover, the economic feasibility of individuals defending feeding sites in water depths to 6 m was likely reduced.

Alexander (1980) observed high levels of aggression among Canvasbacks wintering in coastal South Carolina. Male Canvasbacks dominated females in aggressive encounters that occurred primarily among foraging birds (Alexander 1987). Nichols and Haramis (1980b) speculated that sexual segregation within flocks of wintering Canvasbacks (males being more centrally located within flocks than females) and sexual differences in migration patterns were the result of male dominance. We found little evidence of male dominance of female Canvasbacks in Louisiana. At CL, male aggression towards females was higher than predicted, but Canvasbacks at that location fed in large flocks, and aggressive encounters commonly occurred when a feeding (i.e., diving) bird resurfaced close to another bird, who became the aggressor. Because females fed more than males, they were more likely than males to be the target of aggression. Age also influences Canvasback dominance relationships (Alexander 1987) and might have contributed to an elevated level of female-female aggressive interactions at the MRD. Immature females were more numerous than immature males (W. L. Hohman pers. obs.), and probably required additional feeding time (relative to adults) to sustain a constant rate of fat deposition throughout the winter (Hohman unpubl. data). Thus they were likely to be involved in feeding aggression.

There were differences between study sites in the frequency of disturbance caused by human activities such as fishing, hunting, and commercial and recreational boating. Frequency of disturbance recorded during behavioral observations was higher at CL ($N = 19$ disturbances) than at the MRD ($N = 9$ disturbances), and this was reflected in increased time spent in locomotory and comfort activities at CL. Locomotory and comfort activities of Gadwalls, Mottled Ducks (*Anas fulvigula*), and Tufted Ducks (*Aythya fuligula*) also have been correlated with disturbance (Pedroli 1982; Paulus 1984a, b). Elevated levels of comfort activities recorded in December, especially preening, corresponded to completion of prealternate molt (Austin 1987, Lovvorn and Barzen 1988).

Diurnal time spent feeding varied by sex and study site. Alexander (1980) also found sexual differences in the diurnal time-activity budget of wintering Canvasbacks. Female Canvasbacks may be less efficient for-

agers than males (Takekawa 1987) and require more feeding time. At CL, females consistently spent more time feeding than males, but this was not the pattern in South Carolina (Alexander 1980) or at the MRD (this study). Diving ducks are known to shift from diurnal to nocturnal feeding in response to disturbance (Thornberg 1973, Pedroli 1982). Canvasbacks were known to feed nocturnally at both Louisiana study sites (about 25% of birds collected at night had food in their esophagi; W. L. Hohman, unpubl. data); however, the extent to which birds adjusted nocturnal activities to changes in daytime feeding is unknown.

Physical characteristics of wintering habitats, such as water depth (as affected by tidal cycle and river stage), exposure to wind and waves, and water and air temperature, potentially influenced Canvasback time-activity budgets at the two study sites. We attempted to control for weather factors by collecting behavioral observations from the two study sites simultaneously; however, CL observation areas were deeper, larger, more open, and further inland than those at the MRD. Physical conditions experienced by birds at CL probably were more severe than those at the MRD and may have contributed to study site differences in locomotory and resting activities. Tidal cycle (and river stage) probably influences Canvasback activity patterns at the MRD as it does other waterfowl wintering in coastal habitats (see Paulus 1988). Feeding seemed to be most intensive under low to intermediate tidal conditions, when water levels were shallow enough to permit tipping-up, but data collected here were inadequate to assess quantitatively the effect of tidal cycle (vs river stage) on Canvasback activities.

Activities of wintering Canvasbacks may influence their survival and subsequent reproductive performance. We suggest that the interval between departure from wintering grounds and arrival on areas used for nesting is a critical period for Canvasbacks. Canvasbacks defer pairing until spring migration (Weller 1965, this study); thus, in March and April they simultaneously incur energetic costs of both migration and courtship. Moreover, females initiate prebasic molt (Lovvorn and Barzen 1988) and energy/nutrient storage for reproduction before arrival on nesting areas (Barzen and Serie 1990). Energy reserves accumulated in late winter may be used to meet these costs. Birds at both study sites were fatter in late winter than in early winter, but Canvasbacks at CL were generally leaner than those collected at the MRD (W. L. Hohman, unpubl. data). The extent to which study site differences in Canvasback time-activity budgets influenced fat levels in birds at CL and the MRD, and the consequences of reduced fat levels on overwinter survival and subsequent reproductive performance of Canvasbacks wintering at CL, are still unknown.

ACKNOWLEDGMENTS

We are especially grateful to H. Bateman and J. Tarver, La. Dep. Wildl. Fish. (LDWF); B. Batt, Delta Waterfowl and Wetlands Res. Stn.; and C. Bryan and S. Joyner, USFWS, for their support of the Canvasback research project. We were aided in the field and laboratory by J. Collucy, J. Devries, T. Meis, R. Pritchert, and D. Woolington. The LDWF provided lodging at both study sites. We thank personnel of Pass-a-Loutre and Saline Wildlife Management Areas, and Delta-Breton and Catahoula Lake National Wildlife Refuges for their assistance throughout this study. V. Wright, La. State Univ., provided statistical advice. S. Lauritzen and D. Morais assisted with preparation of the figure. We thank G. Farris, G. Haramis, J. Nassar, K. Reinecke, J. Takekawa, and M. Woodin for their helpful comments on the manuscript.

LITERATURE CITED

- ALEXANDER, W. C. 1980. The behavioral ecology and sociobiology of nonbreeding diving ducks (Aythyini). Ph.D. diss., Clemson Univ., Clemson, South Carolina.
- . 1987. Aggressive behavior of diving ducks (Aythyini). *Wilson Bull.* 99:38–49.
- AND J. D. HAIR. 1979. Wintering foraging behavior and aggression of diving ducks in South Carolina. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* 31:226–232.
- AUSTIN, J. E. 1987. Activities of postbreeding Lesser Scaup in southwestern Manitoba. *Wilson Bull.* 99:448–456.
- BAHR, L. M., JR., R. COSTANZA, J. W. DAY, JR., S. E. BAYLEY, C. NEILL, S. G. LEIBOWITZ, AND J. FRUCI. 1983. Ecological characterization of the Mississippi Deltaic Plain region: a narrative with management recommendations. U.S. Fish Wildl. Serv., FWS/OBS-82/69.
- BARZEN, J. A. AND J. R. SERIE. 1990. Nutrient reserve dynamics of breeding Canvasbacks. *Auk* 107:75–85.
- CHRISTOPHER, M. W. 1987. Wintering waterfowl use of catfish ponds in the Delta region of Mississippi. M.S. thesis, Mississippi State Univ., Mississippi State, Mississippi.
- CONOVER, W. J. 1980. Practical nonparametric statistics, 2nd ed. John Wiley and Sons, New York, New York.
- GOODMAN, D. C. AND H. I. FISHER. 1962. Functional anatomy of the feeding apparatus in waterfowl (Aves: Anatidae). Southern Illinois Univ. Press, Carbondale, Illinois.
- HARAMIS, G. M., J. R. GOLDSBERRY, D. G. MCAULEY, AND E. C. DERLETH. 1985. An aerial photographic census of Chesapeake and North Carolina Canvasbacks. *J. Wildl. Manage.* 49:449–454.
- , J. D. NICHOLS, K. H. POLLOCK, AND J. E. HINES. 1986. The relationship between body mass and survival of wintering Canvasbacks. *Auk* 103:506–514.
- HEITMEYER, M. E. AND L. H. FREDRICKSON. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence Mallard recruitment? *Trans. N. Am. Wildl. Nat. Resour. Conf.* 46:44–57.
- HEPP, G. R., R. J. BLOHM, R. E. REYNOLDS, J. E. HINES, AND J. D. NICHOLS. 1986. Physiological condition of autumn-banded Mallards and its relationship to hunting mortality. *J. Wildl. Manage.* 50:177–183.
- HOHMAN, W. L., D. W. WOOLINGTON, AND J. H. DEVRIES. Feeding ecology of wintering Canvasbacks in Louisiana. *Can. J. Zool.* 68:2605–2609.
- KAMINSKI, R. M. AND E. A. GLUESING. 1986. Density and habitat related recruitment in Mallards. *J. Wildl. Manage.* 51:141–148.

- LOVVORN, J. R. 1987. Behavior, energetics, and habitat relations of Canvasback ducks during winter and early spring migration. Ph.D. diss., Univ. Wisconsin, Madison, Wisconsin.
- AND J. A. BARZEN. 1988. Molt in the annual cycle of Canvasbacks. *Auk* 105:543–552.
- NICHOLS, J. D. AND G. M. HARAMIS. 1980a. Inferences regarding banded Canvasbacks. *J. Wildl. Manage.* 44:164–173.
- AND ———. 1980b. Sex specific differences in winter distribution patterns of Canvasbacks. *Condor* 82:406–416.
- ORTH, R. J. AND K. A. MOORE. 1981. Submerged aquatic vegetation of the Chesapeake Bay: past, present, and future. *Trans. N. Am. Wildl. and Nat. Res. Conf.* 46:299–310.
- PAULUS, S. L. 1984a. Activity budgets of nonbreeding Gadwalls in Louisiana. *J. Wildl. Manage.* 48:371–380.
- . 1984b. Behavioral ecology of Mottled Ducks in Louisiana. Ph.D. diss., Auburn Univ., Auburn, Alabama.
- . 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pp. 135–152 in *Waterfowl in winter* (M. W. Weller, ed.). Univ. Minnesota Press, Minneapolis, Minnesota.
- PEDROLI, J. C. 1982. Activity and time budget of Tufted Ducks on Swiss lakes during winter. *Wildfowl* 33:105–112.
- PERRY, M. C. 1982. Distribution and food habits of Canvasbacks in the Northeast. *Trans. Northeast. Sec. Wildl. Soc.* 38:56–67.
- , W. J. KUENZEL, B. K. WILLIAMS, AND J. A. SERAFIN. 1986. Influence of nutrients on feed intake and condition of captive Canvasbacks in winter. *J. Wildl. Manage.* 50:427–434.
- SAS INSTITUTE, INC. 1987. SAS/STAT Guide for personal computers, Version 6 ed. SAS Inst. Inc., Cary, North Carolina.
- TAKEKAWA, J. Y. 1987. Energetics of Canvasbacks staging on the Upper Mississippi River pool during fall migration. Ph.D. diss., Iowa State Univ., Ames, Iowa.
- THORNBERG, D. G. 1973. Diving duck movements on Keokuk Pool, Mississippi River. *J. Wildl. Manage.* 37:382–389.
- TOME, M. W. AND D. A. WRUBLESKI. 1988. Underwater foraging behavior of Canvasbacks, Lesser Scaups, and Ruddy Ducks. *Condor* 90:168–172.
- WEINS, J. A., S. G. MARTIN, W. R. HOLTHAUS, AND F. A. IVEN. 1970. Metronome timing in behavioral ecology studies. *Ecology* 51:811–813.
- WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). *Auk* 82:227–235.
- WILLS, D. W. 1965. An investigation of some factors affecting waterfowl and waterfowl habitat on Catahoula Lake. M.S. thesis, Louisiana State Univ., Baton Rouge, Louisiana.
- ZWANK, P. J., V. L. WRIGHT, P. M. SHEALY, AND J. D. NEWSOM. 1985. Lead toxicosis in waterfowl on two major wintering areas in Louisiana. *Wildl. Soc. Bull.* 13:17–26.